Chapter for the Handbook of Color Psychology

Chapter 26: Color in competition contexts in non-human animals

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My research interests are easy to explain to anyone who walks into my office. Surrounded by images of mandrills (*Mandrillus sphinx*), one cannot help but ask "why on earth do they look like that?" Male mandrills have spectacular red and sky blue faces, accentuated by grooves that flank the red and divide the blue into ridges. The blue, in particular, accentuates the mandrill's 'grin', an appeasement expression (Setchell & Wickings, 2005). In addition, male mandrills have a red penis, a lilac scrotum, and multi-coloured hindquarters that include red, a deeper blue than the face, violet and lilac skin (Osman Hill, 1970; Setchell & Dixson, 2001a). Female mandrills are muted by comparison to males, but also show bright red and blue skin colour on their faces, the expression of which varies markedly between individuals, and pink skin on their anogenital region (Figure 1).

Mandrills are arguably the most colourful primate, but many other primate species also possess brightly coloured and conspicuous patches of pink/red and blue skin. For example: geladas (*Theropithecus gelada*) have bare patch of pink/red skin on their chest; rhesus (*Macaca mulatta*), Japanese (*Macaca fuscata*) and some other species of macaques have pink or red faces; golden snub-nosed monkeys (*Rhinopithecus roxellana*) have bright blue faces in addition to their golden pelage; and vervets (*Chlorocebus aethiops*) have a blue scrotum and a red penis (Figure 2; Bradley & Mundy, 2008; Dixson, 2012; Gerald, 2003). Furthermore, females of many Old World primate species have bright pink anogenital swellings that develop around the time of ovulation (Nunn, Schaik, & Zinner, 2001) – sometimes so large that zoo visitors turn away and the swollen primates appear to have trouble sitting down. Finally, some primates also show sex differences in pelage, for example adult male gorillas (*Gorilla* sp.) develop a characteristic silver back.

Fig 1: Coloration in mandrills: Top (left to right): Alpha male front, alpha male rear, subordinate adult male face. Bottom: dark-faced female; pink-faced female; female sexual swelling.

In this chapter I review research on the relationship between colour and competition in non-human animals, with particular attention to red coloration in primates (for other species, including birds and fish, see Andersson 1994; Hill 2006). I begin by introducing Darwin's theory of sexual selection as an explanation for the evolution of colour, then examine the circumstances under which colour might signal competitive ability, and how it might do so. Next, I introduce skin colour and primates, before reviewing the evidence for a relationship between skin colour and competition in the two sexes separately. I concentrate on phenotypically plastic skin colour, and within species and within-individual differences, but note that also primates show wonderful coloured pelage (Bradley & Mundy, 2008; Gerald, 2003), including outstanding facial diversity which may function in species recognition (Santana, Lynch Alfaro, & Alfaro, 2012). I end with conclusions and future directions for the study of the influence of colour on the behaviour of non-human animals in contests for mates and resources.

Fig 2: Top (left to right): male geladas have bare patch of pink/red skin on their chest; Japanese macaques have pink/red faces, golden snub-nosed monkeys. Bottom: vervets have a blue scrotum and a red penis.

SEXUAL SELECTION AND THE ADAPTIVE SIGNIFICANCE OF COLOUR

Darwin considered the question of why primates are so colourful in some detail in *The Descent of Man and Selection in Relation to Sex* (Darwin, 1871) and in a subsequent letter to Nature (Darwin, 1876). Conspicuous colour, like other ornaments, is often sexually dimorphic, and males are usually more ornamented than females (Andersson, 1994; Darwin, 1871). These secondary sexual traits – traits not directly required for reproduction, and appearing at puberty – pose a challenge to natural selection, as they advertise rather than conceal and are likely to compromise survival. Darwin called his explanation for these non-utilitarian traits *sexual selection*, based on "the advantage which certain individuals have over other individuals of the same sex and species, in exclusive relation to reproduction" (Darwin, 1871, p256). In other words, the survival costs of sexually selected traits are outweighed by an advantage in fighting other males or attracting females, and thus a higher chance of mating with females, and producing offspring.

Darwin further distinguished between *intra-sexual* and *inter-sexual* selection. Intra-sexual selection occurs for traits that benefit the bearer in competition with members of the same sex for access to mating opportunities (e.g., male-male competition). Inter-sexual selection occurs for traits that make an individual more attractive to members of the opposite sex (e.g., female mate choice). These two concepts remain key pillars of sexual selection theory today (Andersson, 1994), although there is on-going debate as to how to accommodate female-female competition over resources within classical sexual selection theory (Clutton-Brock, 2009; Tobias, Montgomerie, & Lyon, 2012).

COLOUR AS A SIGNAL OF COMPETITIVE ABILITY

Where animals are heavily armed, and both combatants risk injury in physical fights, displays that inform conspecifics about the competitive ability of the bearer can allow the settlement of potentially costly disputes without escalated combat (Andersson, 1994; Bradbury & Vehrencamp, 1998; Rohwer & Ewald, 1981). Such 'badges of status' include colour traits in birds (Rohwer & Rohwer, 1978; Rohwer, 1975, 1977), fish (Barlow & Wallach, 1976; Barlow, 1973), and lizards (Thompson & Moore, 1991).

If colour is to function as a reliable signal of competitive ability, then there should be a cost associated with cheating that outweighs the benefits of displaying an inappropriate signal. Various mechanistic hypotheses have been proposed to explain signal reliability. Signal honesty may be maintained by social costs, if only high quality males are able to withstand repeated challenges, and tests of their fighting ability (Rohwer & Ewald, 1981; Rohwer & Rohwer, 1978; Rohwer, 1977). Alternatively, cheating may be impossible for lower quality individuals due to the costs incurred in producing colour, which, therefore, provide an honest signal of the genetic and/or phenotypic quality of the bearer. For example, conspicuous colour may expose the bearer to increased predation risk, with dominant individuals being better able to escape (Endler, 1980). Other hypotheses require the production of colour to involve physiological costs, such that colour signals health or condition. For example, colour may reflect dietary access to pigments (Hill, 2006), the bearer's ability to overcome a handicap (Zahavi, 1975), resist pathogens (Hamilton & Zuk, 1982), cope with the immunosuppressive effects of testosterone (Folstad & Karter, 1992) or the costs of oxidative stress (von Schantz, Bensch, Grahn, Hasselquist, & Wittzell, 1999); or the ability to withstand stressors (Buchanan, 2000; Hillgarth & Wingfield, 1997; Westneat & Birkhead, 1998). At a genetic level, colour may signal overall genetic diversity and fitness (Brown, 1997), or genetic quality related to particular coding loci, such as the major

histocompatibility complex (MHC), a multigene family that plays a critical role in the immune response (Penn & Potts, 1998). In each case, low quality individuals would be unable to sustain the physiological costs associated with producing a colour signal.

COLOUR IN PRIMATES

Why study colour and competition in primates? Perhaps the first answer is that we (humans) are primates. Thus, the other primates provide a natural comparative context for our own evolution. We have already seen that primates show great diversity in coloration. They are also the only mammals to exhibit bright coloration, both in skin and pelage. This may be linked to their gregarious social systems, which may promote sexual selection for visual advertising (Fernandez & Morris, 2007). Unlike other colourful vertebrates, such as birds, fish and lizards, primates live in particularly complex social environments (Mitani, Call, Kappeler, Palombit, & Silk, 2013). Primate social systems range from solitary, nocturnal mouse lemurs to the highly socially complex multi-male, multi-female societies of chimpanzees, with mating systems that encompass monogamy, polygyny, polyandry and polygynandry (Mitani et al., 2013). This range of social and mating systems makes for interesting cross-species comparisons of the relationship between colour and competition, as well as providing the potential to study the interactions between signals and social knowledge (Bergman & Sheehan, 2012). However, until recently, there have been few studies of primate coloration, in contrast with other colourful taxa, such as birds and fish, (Andersson, 1994; Hill & McGraw, 2006).

Bright skin colour in primates is pink/red, blue, or a combination of the two; colours which are easy to produce, in evolutionary terms (Grubb, 1973). Pink/red is thought to be due to the colour of oxygenated haemoglobin in highly-vascularised, blood-filled tissues (Rhodes et al., 1997). In contrast, blue is a structural colour, due to the physical interactions of light waves with biological structures. Although often attributed to incoherent, Rayleigh or Tyndall scattering, the blue is actually a result of "coherent scattering from quasi-ordered arrays of dermal collagen fibre" (Prum and Torres, 2004 p2164). Hue differences between skin patches appear to be a result of differences in the size and spacing of dermal collagen arrays (Prum & Torres, 2004). Red skin occurs in the Cercopithecinae (including in Hamadryas baboons, macaques, vervets, geladas, mandrills and drills) and Colobinae (including in proboscis monkeys), as well as in New World monkeys (including in some species of howler monkeys, spider monkeys, sakis and uacaris), while blue skin has evolved at least twice, in *Mandrillus* and *Cercopithecus* (both are Cercopithecine genera, Prum & Torres, 2004). I am not aware of

any evidence of cosmetic or adventitious colours in any non-human primates, unlike humans and birds (Montgomerie, 2006a), with the possible exception of chest-staining as a byproduct of scent-marking in sifaka (Lewis & van Schaik, 2007).

Finally, the primate visual system is relatively well described. Old World monkeys, in particular, have very similar, although not identical, trichromatic colour vision to humans (Jacobs & Deegan, 1999; Yokoyama & Yokoyama, 1989). This makes primates easier to study than other brightly coloured vertebrates, including birds and fish, which are ancestrally tetrachromatic, with a colour space of higher dimension than in humans (Cuthill, 2006). Phylogenetic reconstruction suggests that trichromatic vision seems likely to have evolved to improve foraging performance in primates, providing a pre-existing bias than then led to the evolution of red traits (Fernandez & Morris, 2007). The evolution of red colour is also linked to gregarious social systems, which may facilitate the comparison of competitors (Fernandez & Morris, 2007). Interestingly, primate colour vision is near optimal for discriminating blood-related changes in skin colour (Changizi, Zhang, & Shimojo, 2006), although the evolution of trichromacy preceded that evolution of red skin (Fernandez & Morris, 2007).

COMPETITION AND COLOUR IN MALE PRIMATES

Bright male skin coloration is concentrated in primate taxa with polygynous and polygynandrous mating systems (Dixson, 2012). Male-male competition for access to receptive females is high in such species, where males compete either to monopolise access to a group of females if they are able to exclude all other males from a group, or to mate in multi-male, multi-female groups. Fights can be devastating for the individuals involved and contest competition between two individuals may benefit a third individual if both contestants are wounded or exhausted.

The link between competition and colour in male primates has been investigated in five species of non-human primate.

Mandrills

> *"No other member in the whole class of mammals is coloured in so extraordinary a manner as the adult male mandrill (*C. mormon*). The face at this age becomes of a fine blue, with the ridge and tip of the nose of the most brilliant red. According to some authors, the face is also marked with whitish stripes, and is shaded in parts with black, but the colours appear to be variable. On the forehead there is a crest of hair, and on the chin a yellow beard. "Toutes les parties superieures de leurs cuisses et le*

grand espace nu de leurs fesses sont egalement colores du rouge le plus vif, avec un melange de bleu qui ne manque reellement pas d'elegance." When the animal is excited all the naked parts become much more vividly tinted. Several authors have used the strongest expressions in describing these resplendent colours, which they compare with those of the most brilliant birds. Another remarkable peculiarity is that when the great canine teeth are fully developed, immense protuberances of bone are formed on each cheek, which are deeply furrowed longitudinally, and the naked skin over them is brilliantly-coloured, as just-described. In the adult females and in the young of both sexes these protuberances are scarcely perceptible; and the naked parts are much less bright coloured, the face being almost black, tinged with blue."* (Darwin 1871 pp.292-3).

**all the upper portion of their thighs and their large bare rumps are also the most colorful bright red, with a very elegant mixture of blue (author's translation)*

Mandrills are semi-terrestrial monkeys that live in very large multi-male, multi-female groups in the dense rainforests of central Africa (Abernethy, White, & Wickings, 2002; Grubb, 1973). Both colour and the extent of colour varies for red, pink and lilac skin on the face, hindquarters and genitalia, and values for the multiple skin areas correlate in adult males (Setchell & Dixson, 2001a). The different areas of colour also develop simultaneously following puberty, although the pace of development varies among males (Setchell & Dixson, 2002). Mandrills mate moderately seasonally (Setchell & Wickings, 2004a), and male testosterone increases during the mating season, but males remain colourful all year round (Setchell & Dixson, 2001b).

The general correlations across the various areas of colourful skin in male mandrills have led to a focus on the red of the muzzle as a measure of colour that is relatively easy to define (in contrast to the blended colours of the hindquarters, for example). However, there are also regional differences in changes in skin colour with rank, with facial and genital red reducing more than the perianal red patch in mandrills (Setchell & Dixson, 2001c), allowing for the possibility that different areas of skin convey different information to perceivers. In adult male mandrills, the mid-nasal strip varies in colour from pale pink to a vibrant blood red, and in extent from a red stripe on the muzzle to all over the eye area, lower lips and ears, with 'bleeding' into the blue paranasal ridges (Setchell & Dixson, 2001a). The alpha male is usually, but not always, the most colourful male in a group (Setchell & Dixson, 2001a, 2001c; Setchell, Smith, Wickings, & Knapp, 2008). Challenger subordinate males who defeat a top-

ranking male subsequently increase in both red colour and the extent of red colour (Setchell & Dixson, 2001c; Setchell et al., 2008). Thus, high rank leads to an increase in colour, rather than the other way around.

The extent of red coloration increases with tenure as alpha male (Setchell, unpublished data), providing further potential information concerning competitive ability to the perceiver. Colour, and the extent of coloration, decrease in defeated, post-alpha males, but the difference is less extreme than the gain that comes with attaining alpha rank (Setchell & Dixson, 2001c). Colour in deposed alpha males does not reduce to the level of a male that has never been alpha. For example, post-alpha males may retain dots of red in their blue paranasal ridges), suggesting that post-alpha males continue to signal the traits that allowed them to hold top rank (Setchell et al., 2008), and possibly some permanent changes in gene expression and skin receptor populations.

Like many secondary sexual ornaments in male vertebrates (Andersson, 1994), red colour is related to testosterone in male mandrills (Setchell et al., 2008). However, colour is not closely related to overall body size, or weaponry in adult males, as alpha males are not always the heaviest or largest males, and do not necessarily have the longest canine teeth among the males in a group (Setchell, Wickings, & Knapp, 2006b). This suggests that relative testosterone levels are more important in male-male interactions than are small differences in size, perhaps because all males are well-armed, with long canine teeth, making motivation to fight more important than body size in male encounters.

Socially-induced suppression of colour in subordinate male mandrills may be adaptive in reducing male competition and facilitating alternative mating tactics, as part of a conditional mating strategy (Setchell & Dixson, 2001a). In support of this possibility, rank instability leads to an increase in testosterone (Setchell et al., 2008) and colour (Setchell & Dixson, 2001c) in all males, and even the lowest-ranking males can develop maximal colour if dominant males are removed (Setchell & Dixson, 2001a). In addition to reduced testosterone levels, androgen-sensitive target tissues may also differ between dominant and subordinate males. For example, subordinates may show reduced gene expression in target tissues and thus reduced hormone receptor populations or reduced expression of the aromatase required to aromatise testosterone (Setchell & Dixson, 2001a).

Mandrills have long canine teeth, and escalated fights can occasion substantial costs to both combatants, including serious injury and death (Setchell et al., 2006b). Observational data suggest that male mandrills attend to colour in rivals: unidirectional submission occurs in male dyads with clear differences in red, but threats, contact aggression and unresolved

'standoff' encounters are more common where males are similar in colour, and thus unable to determine outcome of the encounter based on simple rules, suggesting that red coloration acts as a badge of status in male mandrills (Setchell & Wickings, 2005). However, it is not possible to separate the influences of colour and rank statistically in these data, and experiments are needed to determine whether colour alone determines male interactions. Combining stimuli representing familiar and unfamiliar animals would also allow us to disentangle social knowledge from the effect of red.

Mandrill red appears to be a dynamic trait that mirrors changes in male physiology relatively rapidly, although not as rapidly as blushing in humans, dynamic colour in chameleons (Ligon & McGraw, 2013), carotenoid-derived bill colour in birds (Faivre, Grégoire, Préault, Cezilly, & Sorci, 2003), or as fast as Darwin suggested. As red skin colour responds to changes in social status, it appears to indicate current state, rather than individual quality (Setchell & Dixson, 2001c). Nevertheless, gaining high rank necessitates good genes, in addition to a degree of good fortune (e.g., a poorer quality male may gain high rank if two other males fight and injure one another, or if there are simply few rival males).

The mandrill is the only primate species in which the relationships among skin colour, parasites, body condition, immune parameters, genetic quality, androgens and glucocorticoids have yet been examined in detail (Setchell, Charpentier, Abbott, Wickings, & Knapp, 2009; Setchell, Smith, Wickings, & Knapp, 2010). Red is not related to parasite load or to haematological parameters in individual males (Setchell et al., 2009). There is, thus, little support for the Hamilton-Zuk hypothesis of parasite-mediated sexual selection (Hamilton & Zuk, 1982) as an explanation for male colour in mandrills. However, correlational studies provide weak tests of the relationship between ornaments and condition (Cotton, Fowler, & Pomiankowski, 2004), and improved measures of immune system quality are needed for a robust test of the hypothesis that colour signals health in this species. Red is also unrelated to either overall genetic diversity or to MHC diversity (Setchell et al., 2009). However, red is related to the possession of specific MHC genotypes, providing some support for the hypothesis that red colour advertises 'good genes' in mandrills, if these genotypes are beneficial in terms of health. Finally, although male mandrills with higher glucocorticoid levels suffered a higher diversity of parasite infection, we found no significant relationship between glucocorticoids and red colour, suggesting that glucocorticoids do not play a simple role in translating physical health into colour (Setchell, Smith, et al., 2010) and providing little support for the stress-mediated hypothesis for the evolution of sexual signals in this species (Buchanan, 2000; Evans et al., 2000; Poiani et al., 2000).

In contrast to red and related colours (purple, violet, pink), blue appears invariable in adult mandrills when measured using colour charts (Setchell & Dixson, 2001a), although, like red, it increases during adolescence (Setchell & Dixson, 2002). However, a recent study, using more sophisticated methods, has shown that higher-ranking males display more saturated blue as well as red, and consequently a stronger contrast between the two colours, than lower-ranking males (Renoult, Schaefer, Sallé, & Charpentier, 2011). Both the mean value and the variance are greater for the blue-red contrast than for either blue or red saturation alone, suggesting that the contrast is easier for the perceiver to detect than either colour alone (Renoult et al., 2011). Detailed studies of skin biopsies show that variation in the brilliance and saturation of the blue colour on the mandrill's face may be correlated with the thickness of the collagen arrays that produce the colour, suggesting that variation collgenocyte activity in the dermis may underlie variation in blue colour (Prum & Torres, 2004). As yet we have no data to investigate potential hormonal correlates of skin blue colour.

Taken together, these results suggest that red, blue, and the contrast between them reflect male rank, and that alpha males are the most colourful mandrills. Alpha males also sire the most offspring in mandrills (Charpentier et al., 2005; Setchell, Charpentier, & Wickings, 2005), providing a link between colour and reproductive success. In the wild, mandrills live in very large, fluid groups, in a deep rainforest environment and male group membership may be transient (Abernethy et al., 2002). Their blue colour is conspicuous against the background colours of their environment (Renoult et al., 2011; Sumner & Mollon, 2003). These conditions may have favoured the evolution of exaggerated coloration as a badge of status where rivals are either unfamiliar with one another (Preuschoft & van Schaik, 2000), or as a current state signal, where individuals lack up-to-date social knowledge of rivals (Bergman & Sheehan, 2012).

Drills

Like mandrills, the only other species of *Mandrillus*, the drill (*Mandrillus leucophaeus*), also lives in the central African rainforest (the distributions of mandrills and drills appear to be split by the Sanaga River in Cameroon, Grubb, 1973). Drills may also form very large groups (Wild, Morgan, & Dixson, 2005), and also exhibit striking coloration. However, in contrast to the red and blue faces of mandrills, drills have shiny black faces set off by a white fringe of hair. Males have a horizontal red stripe under the lower lip, a red penis and extensive red above the penis, extending down the legs (which may be more extensive than in mandrills), a lilac scrotum, and blue, violet and pink on the hindquarters (Marty, Higham, Gadsby, & Ross,

2009; Osman Hill, 1970). As in mandrills, red coloration is linked to testosterone: experimental administration of testosterone led to 'flushing' of the lip and groin (Zuckerman & Parkes, 1939). Male lip and groin coloration correlate positively (Marty et al., 2009), but there are no studies relating these two areas to the (complex) colour of the hindquarters. As in mandrills, higher-ranking males are more colourful in both colour saturation and the extent of colour (Marty et al., 2009).

Vervets

Vervet monkeys are smaller, semi-terrestrial monkeys that are widely distributed in sub-Saharan Africa. Adult males have a red penis, and a blue/green scrotum (Darwin, 1871) which they display to other males in a characteristic 'red, white and blue display' in which a dominant male walks around a submissive male with his tail raised (Henzi, 1985; Struhsaker, 1967). Sub-species differ in blue coloration, from white or pale blue, via sky blue, to blue-violet (Osman Hill, 1966), and also in how maturation affects blue colour: blue becomes lighter with age in both *Chlorocebus aethiops pygerythrus* and *C. a. sabaeus* males, but the former become bluer while the latter become less blue with increasing age (Cramer et al., 2013). The blue colour of the scrotum also varies between individuals of the same population (Henzi, 1985; Isbell, 1995).

An early experimental study suggested that scrotal colour varies with dermal hydration, because injecting water into scrotal tissue led to increased pallor, and compressing the tissue with forceps made the blue colour deeper (Price, Burton, Shuster, & Wolff, 1976). The latter is also true for mandrill facial blue (Setchell, unpublished observations). However, a more recent study notes that there is no evidence that natural variation in vervet skin colour is related to dermal hydration (Prum & Torres, 2004). Variation in vervet scrotal colour is unlikely to be closely related to variation in testosterone levels, as castration does not affect blue in the closely-related talapoin (*Miopithecus talapoin*, Dixson & Herbert, 1974). Moreover, blue does not vary with season in either vervets (Henzi, 1985; Isbell, 1995) or patas monkeys (*Erythrocebus patas*, Bercovitch, 1996), despite large changes in testosterone between the mating and non-mating season in the latter species. However, social conditions do affect colour in vervets: the scrotum pales over a couple of weeks in captive males when they are introduced into a new group and face aggression from higher-ranking males (Gartlan & Brain, 1968). Trapping vervets also leads to increased pallor (Gerald & McGuire, 2008), although quarantining male patas monkeys does not alter scrotal color (Bercovitch, 1996). Finally, scrotal colour correlates with serotenergic function, specifically males with blue or

purple coloured scrota had higher cerebrospinal fluid concentrations of 5-hydroxyindoleacetic acid (CSF-5-HIAA) than those with green scrota (Gerald & McGuire, 2008). CSF-5-HIAA, in turn, correlates with aggression (e.g., Fairbanks et al., 2001, 1999), suggesting a possible relationship between colour and aggressive behaviour.

An elegant experimental study split captive male vervets into two categories, based on their scrotal coloration: pale and dark (Gerald, 2001). Pale males were assigned to three experimental groups: pale; painted males, painted with spray paint to match dark males; and control males, painted with clear, transparent spray paint. Scrotal colour predicted the outcome of experimental introductions between males of similar size, with dark males more likely to win encounters than pale males. Same-colour pairs were more likely to interact aggressively than pairs that differed in colour, also supporting the predictions of a status signal. When a pale male was paired with an artificially dark male, pairs showed less aggression than pairs of pale males, providing further support for blue as a status signal. However, painted males did not dominate pale males, contrary to prediction, and possibly due to behavioural attributes of the painted males. There was no evidence that males distinguished between naturally and artificially dark males. Surprisingly, these results remain the only experimental evidence that colour affects social status in non-human primates.

Although data for captive animals suggest a link between social conditions and scrotal colour, and wild vervets have easily detectable, linear hierarchies, studies of wild groups have found that blue scrotal colour does not vary significantly with rank (Henzi, 1985; Isbell, 1995). It may be that age and size differences are the primary determinants of rank among wild males, rendering colour differences less important. Further study of the relationship between rank and colour in existing groups is clearly needed, using modern methods to quantify colour, testing for colour change in relation to changes in dominance rank, and linking colour phenotype to reproductive success (Gerald, 2001). Moreover, no study has yet included the red component of the vervet multi-component display. It seems very likely that the components interact to increase the potential information content of the signal, either by adding additional information, or by increasing contrast, as in the mandrill's nose (Renoult et al., 2011).

Rhesus macaques

Adult male rhesus macaques experience reddening of the skin on the face, genitals and hindquarters during the mating season (Baulu, 1976; Sade, 1964; Vandenburgh, 1965). The degree of coloration is highly variable among individuals (Rhodes et al., 1997; Waitt, Gerald,

Little, & Kraiselburd, 2006), ranging from light pink to dark red, with more variation in genital colour than on the face or rump (Higham, Pfefferle, Heistermann, Maestripieri, & Stevens, 2013). Castration causes a decline in skin colour, although it does not reach normal body skin colour, possibly due to adrenal androgens (Vandenburgh, 1965). Experimental administration of both testosterone and oestrogen also increases reddening of the skin in these areas, but not of other areas (Vandenburgh, 1965), as a result of increased epidermal blood flow (Rhodes et al., 1997). Treatment with an aromatase inhibitor (fadrozole) reduces red colour, suggesting that the change in red results from the aromatization of testosterone to oestrogen (Rhodes et al., 1997).

As in mandrills and drills, the red colour of the three body regions in rhesus macaques correlates positively both between and within individuals for face/genitalia and genitalia/hindquarters comparisons, although only within individuals for face/hindquarters comparisons (Higham et al., 2013). This weaker relationship allows for the possibility that the face and hindquarters may encode different information (Higham et al., 2013), possibly mediated via tissue-specific differences in enzyme activity or receptor populations, as suggested for mandrills (Setchell & Dixson, 2001c).

Despite the general, seasonal relationship between red colour and testosterone in male rhesus macaques, and an early note that the sex skin pales when a breeding male loses rank (Carl B. Koford pers. comm. in Vandenburgh, 1965), a recent study found no evidence that red coloration is linked to rank or to androgen levels during the mating season (Higham et al., 2013). No experimental studies have yet been published that examine male-male relationships in relation to red in rhesus macaques, although adult males do attend to female red coloration (Higham et al., 2011; Waitt et al., 2006). Males also attend to red more generally: adult males were more likely to choose food from an experimenter wearing green than one wearing red, regardless of the sex of the experimenter, and were also more likely to take food from a male experimenter wearing blue than from a female experimenter wearing red (here the sex effect was not tested) (Khan, Levine, Dobson, & Kralik, 2011). The authors interpret this evidence as evidence that red signals dominance in the macaques (Khan et al., 2011). However, this interpretation conflicts with the results of the observational studies described above, where red does not correlate with rank (Higham et al., 2013).

Geladas

Both male and female geladas have a patch of red skin on their chest and neck. Geladas live in a multi-level society, with very large groups made up of small units of females and their

offspring accompanied by one ‘leader’ male and possibly 1-2 ‘follower’ males. Followers are subordinate to the leader, and are either young males that have not yet acquired a unit, or older, former leader males. Other males live in all-male groups (Dunbar & Dunbar, 1975; Dunbar, 1984; Snyder-Mackler, Bergman, & Beehner, 2012). The chest patch is redder in leader males and prime-aged adult males than in other males (Bergman & Beehner, 2008; Bergman, Ho, & Beehner, 2009). Furthermore, males living in large reproductive units, with more mating opportunities, have redder chest patches than those in small units, and fewer mating opportunities (Bergman et al., 2009). Similar to alpha male takeovers in mandrills, when a male challenges a leader male and takes over, he reddens, while the previous male fades rapidly (Bergman et al., 2009; Dunbar, 1984).

Interestingly, male colour varies with activity level in gelada, being redder within 20 minutes of activity in comparison with non-active periods (Bergman et al., 2009). This suggests a possible connection between bare patches of skin and temperature regulation in large primates, and thus a possible evolutionary history for red skin. It also provides a pleasing link to Darwin’s report that ‘excited’ mandrills become more vivid (1871, p.293). No similar test has been undertaken in mandrills, but if such an effect exists, my long-term observations of male mandrills suggest that it is not dramatic.

Summary of competition and colour in male primates

This review of the literature allows us to draw some conclusions regarding male colour and competition in primates:

1. Studies to date suggest that where a species has more than one area of skin of the same colour, then values generally correlate, and are likely to provide the same information. However, exceptions occur in both mandrills and rhesus macaques, allowing for the possibility that different skin patches encode different information. Where animals display more than one colour, these also convey similar information, but colour contrast increases the information content of the signal (Renoult et al., 2011).
2. Correlational studies suggest that red skin colour may act as a badge of status in some primate species, indicating male rank (mandrills, drills) and status (geladas), and testosterone (mandrills). The placement of these colour patches on the front of the animal also suggests that they act as badges (Ortolani, 1999), although mandrills also have bright hindquarters. Although social organisation and mating systems differ between *Mandrillus* species and geladas, all three species live in large, fluid, groups, in which males may lack current knowledge of their rivals’ status, promoting the

evolution of status signals.

3. Red does not predict male relationships in gelada and mandrills in one important respect: subordinate males that challenge and defeat the alpha male in mandrills, or a leader male in geladas, are less colourful than the target male when the takeover occurs (Bergman et al., 2009; Setchell et al., 2008). Thus it appears that an alpha male mandrill signals his top rank, while a leader male gelada signals both leader status and the number of females in 'his' unit, but the challenger in both species does not signal his challenge until he is successful. Attaining alpha or leader status results in higher colour, probably because winning encounters, and the ensuing sexual access to females both lead to increased testosterone levels (Dixson, 2012). In other words, red colour signals that a male has gained top rank and can bear any costs of dominance. In this respect, it is interesting that alpha male mandrills continue to increase in the extent of red coloration as their tenure increases. This supports hypotheses that suggest males pay a social cost of high colour: colourful, alpha males are subject to repeated tests, and remain red if they win these encounters.
4. Red does not correlate with body size among adult mandrills, possibly because testosterone levels, and willingness to fight, are more important than small differences in body size in such well-armed rivals. No study has yet directly compared red colour with rates of aggression, but threats, chases and fights all occur more often in high-ranking (i.e., red) males than in low-ranking (i.e., paler) males.
5. In contrast to male mandrills and drills, it remains unclear whether and how red skin colour functions in male-male interactions in rhesus macaques, in which red does not reflect rank or individual testosterone levels. Possible explanations for this difference lie in the differences in social and mating system between rhesus and *Mandrillus* species. Both species can live in very large multi-male, multi-female groups (>200 in Higham et al.'s study group), but rhesus group membership may be less fluid than in mandrills, where large groups may form sub-groups (Harrison, 1988). Both species breed seasonally, but while rhesus males' redden during the mating season, when their testes increase in volume by 50–70% and they undergo marked increases in circulating testosterone (Sade, 1964; Wickings & Nieschlag, 1980), mandrills are coloured all year round, with much smaller increases in testes size and testosterone during the mating season (Setchell & Dixson, 2001b). This suggests that male competition is important year-round in mandrills, but less so in rhesus. Competition appears to be lower overall in rhesus macaques, which are less sexually dimorphic than mandrills, in

both body size and canine size (Plavcan, 2001), suggesting that males experience less direct competition over rank and mating access. In line with this, rank-related reproductive skew is far lower in rhesus than in mandrills (Berard, Nürnberg, Epplen, & Schmidtke, 1993; Dubuc, Muniz, Heistermann, Engelhardt, & Widdig, 2011; Widdig et al., 2004).

6. We only have experimental evidence for one species (vervets) that males attend to differences in the coloration of rivals (Gerald, 2001). However, while this is strong evidence that blue skin acts as a badge of status in this species, no relationship between rank and colour has been found in the wild. There is, thus, a great deal more work to be done to determine whether male primates perceive, and respond to, signal variation in other males.
7. Finally, although anecdotal reports suggest that parasite infection results in fading of the bright red head of the bald uacari (*Cacajao calvus*) (Ayres, 1996; Lasry & Sheridan, 1965) and poor nutrition leads to fading of blue scrotal coloration in vervets (Isbell 1995), detailed studies of the relationships between skin colour and individual condition and quality are available for only one species – mandrills. These studies are correlational, so provide weak tests of the hypotheses. Nevertheless, they found no support for a relationship between colour and health, or for the stress-mediated immunocompetence handicap hypothesis, although there was some support for the notion that colour advertises the possession of particular immune genes.

COMPETITION AND COLOUR IN FEMALE PRIMATES

Until relatively recently, studies of ornaments, including colour, have focused on males (Andersson 1994). The evolution of female ornaments is less well understood than that of males, and has, arguably, been limited by the typical view of Darwinian sexual selection, in which males compete for mates while females choose. Competition among females does not map onto the classical sexual selection framework easily, as in many cases females are more limited by access to resources than they are by access to mates (Tobias et al., 2012). For example, female primates gestate and suckle offspring, usually born one at a time, and provide the vast majority of offspring care. Female reproductive success is related to dominance rank (Pusey, 2013), but the number of offspring a female produces is more limited by the resources needed to fuel gestation and lactation than by competition for matings (Trivers, 1972). Nevertheless, whether inter-sexual selection occurs for mates or for

resources, the outcome in terms of the evolution of signals of competitive ability may be similar.

Following Darwin (1871), female ornaments, including colour, are often assumed to be non-adaptive by-products of selection for ornamentation in males, as the two sexes share most of the genome in a species, and thus both inherit the genes for ornaments (Lande, 1980). Unless selection against female ornaments is strong, they are expected to show vestigial or rudimentary ornaments. However, comparative evidence suggests that female ornament expression is not strongly constrained by selection on males (T. Price & Birch, 1996), suggesting that we should seek adaptive explanations for female traits. Moreover, females may also possess ornaments that do not exist in males, including bright pink anogenital swellings in female primates (Dixson, 2012). In such cases, female traits clearly require an adaptive explanation. Indeed, studies of birds suggest that females do use colour in intra-sexual communication (Amundsen, 2000; Amundsen & Parn, 2006).

As in males, conspicuous skin colour in female primates is concentrated in polygynous and polygynandrous species. Skin colour occurs on the face, anogenital area and paracallosal skin, as well as on the chest in gelada (Dixson, 2012). Most studies of skin colour in female primates have been conducted in the context of inter-sexual communication, and investigate variation with age (Altmann, 1973; Gauthier, 1999; Setchell & Wickings, 2004b; Strum & Western, 1982) or across the female reproductive cycle (e.g., Baulu, 1976; Bielert et al., 1976; Czaja et al., 1977; Dubuc et al., 2009; Dunbar and Dunbar, 1977; Fujita et al., 2004; Gauthier, 1999; Gerald et al., 2008; Higham et al., 2008; Setchell et al., 2006a). Although these studies suggest that female colour contains information about female status, they do not contribute to our understanding of whether females use colour in a competitive context. However, a few studies have incorporated the question of female-female competition, by investigating the relationship between female colour and dominance rank, while two experiments explore whether females attend to differences in female colour.

Female colour and dominance rank

Facial colour in female mandrills varies from entirely black-faced to a bright-pink mid-nasal stripe with blue paranasal ridges, and the range of colour overlaps with that of males considerably (Setchell et al., 2006a). Neither facial nor anogenital colour are related to female rank in mandrills (Setchell et al., 2006a; Setchell & Wickings, 2004b), and the same is true for anogenital colour in baboons (Higham et al., 2008). Non-one has yet tested how female colour relates to testosterone. Anogenital swelling colour in mandrills relates to measures of

body condition (Setchell & Wickings, 2004b), although face colour does not (Setchell et al., 2006a). Neither anogenital nor face colour correlate with measures of reproductive success in female mandrills (Setchell et al., 2006a; Setchell & Wickings, 2004b), unlike in males. These findings are unsurprising, given that male and female reproductive priorities also differ greatly in mandrills. Moreover, while male rank is determined via contest competition, female mandrills inherit their mother's rank, and their rank is unrelated to body size or condition (Setchell, 1999).

Do females attend to female colour?

Two experimental studies of rhesus macaques have investigated whether females attend to colour in other females. As in males, the sexual skin of female rhesus macaques reddens during the mating season. The first study exposed females to computerised images of conspecific female faces and hindquarters that had been manipulated for colour (red versus non-red), within the natural range of colour variation. The females attended visually more to reddened faces and hindquarters than to non-red equivalents, suggesting that female colour may be biologically meaningful to other females (Gerald, Waitt, Little, & Kraiselburd, 2007). Combined with a study showing that facial skin colour is informative concerning the timing of the fertile phase in this species (Dubuc et al., 2009), this suggests that females may obtain information about other females' cycle status by attending to facial colour.

Female rhesus macaques also show bright facial coloration during the last trimester of pregnancy (Rowell, 1972). In the second experimental study, Gerald et al. (2008) presented adult rhesus macaques with images of female faces with and without pregnancy coloration. Female gaze duration did not differ between the two conditions, but subjects of both sexes showed more appeasement behaviour to faces with pregnancy coloration than to non-pregnant stimuli, providing limited evidence that females may attend to this colour.

Summary of competition and colour in female primates

The small handful of studies that have examined the link between colour and competition in female primates allow us to draw the following conclusions:

1. Unlike in males, there is no documented evidence of a link between rank and colour in females, reflecting different selective processes and the different reproductive priorities of the two sexes.
2. However, colour does correlate with other aspects of female status (age, reproductive status) and experimental evidence that females attend to female colour suggests that

females may use colour in intra-sexual communication, although as yet, we do not know how.

3. The possibility remains that colour is a vestigial, correlated response to selection for colour in males, with no function of its own. However, no-one has suggested that colour in male macaques is a correlated response of a female signal, despite the fact that no function has yet been identified for male colour. This observation may highlight a bias in our approach to ornaments.

CONCLUSIONS AND FUTURE DIRECTIONS

Research on competition and colour in primates has lagged behind that on other colourful taxa. However, the studies of the relationship between competition and colour in non-human primates reviewed here suggest that the red effect in humans has evolutionary roots in our primate ancestors. They also suggest that while there is often a relationship between red colour and status (e.g., alpha male mandrills, leader male geladas), this is not always the case (rhesus macaques), and that the same does not apply to females.

There is a general trend towards more sophisticated measures of primate colour. As in birds (Montgomerie, 2006b), the study of primate colour began with subjective rankings and descriptions (J. S. Price et al., 1976; Wickings & Dixson, 1992), then progressed to visual comparison to colour charts (Gauthier, 1999; Gerald, 2001; Setchell & Dixson, 2001a, 2001b, 2001c). This works well for categories (e.g., dark vs. pale) and for species with large individual differences in colour. However, digital imagery provides better quantitative data, when corrected for ambient lighting (M S Gerald, Bernstein, Hinkson, & Fosbury, 2001; Martin Stevens, Parraga, Cuthill, Partridge, & S.Troscianko, 2007). More sophisticated methods include spectrometry (Renoult et al., 2011; Sumner & Mollon, 2003). Future studies should also, ideally, account for the species' visual system (Stevens, Stoddard, & Higham, 2009), as well as the visual environment in which a signal occurs, to obtain a primate's eye view of their world. For example, theory predicts that red signals in forest shade should include blue or blue-green, to be most conspicuous (Thery, 2006). This is exactly what a study of mandrills found (Renoult et al., 2011), but prompts the question of why closely-related drills, which inhabit a very similar habitat, have very different, but equally striking, shiny black faces with a white ruff.

Bright colour appears to occur predominantly in primate species with very large group sizes, including mandrills, drills, geladas, red uacaris, and Hamadryas baboons, where animals may have limited, or no, social knowledge of their rivals, and sexual selection is

strong (Setchell & Kappeler, 2003). Inter-specific comparative studies are clearly needed to examine the evolutionary correlates and history of skin colour, and variation in skin colour, in detail.

The question of whether and how colour indicates phenotypic or genetic quality in primates, beyond a relationship between red and testosterone levels, has barely been addressed. This is in contrast to both observation and experimental studies linking colour with health status and genetic diversity in non-primates (Andersson, 1994; Foerster, Delhey, Johnson, Lifjeld, & Kempenaers, 2003; Herdegen, Dudka, & Radwan, 2014; Hill, 2006; Johnstone, 1995; Müller & Ward, 1995; Oosterhout et al., 2003; Zuk, 1992). Prum & Torres (2004) suggest that blue skin effectively has no physiological costs, as the collagen that results in the structural colour is a ubiquitous protein, and that the spacing of the collagen fibres is unlikely to be sensitive to perturbation in the bearer's health or condition, suggesting that social costs maintain any signal value of blue colour. However, blue ridges may serve to highlight symmetry in the male mandrill's muzzle, for example, which may reflect the ability to cope with developmental stress (e.g., Møller & Hoglund, 1991). The potential physiological correlates of red have only been investigated in mandrills, and these studies generally provide little support for the hypothesis that red colour signals condition in this species. However, these tests are correlational and improved tests of immunocompetence (e.g., Drury, 2010) and experimental studies are needed before we can draw conclusions concerning the relationship between genotype, phenotype and colour.

Colour signals in primates are made up of a combination of elements, as in the multiple skin colours displayed by mandrills, which also have a yellow beard. Such combinations can act as redundant (or back-up) signals, reflecting the same quality of the bearer, or multiple messages about different qualities of the bearer (Candolin, 2003). The multiple regions of colour that (mainly) correlate in mandrills (Setchell & Dixson, 2001a), drills (Marty et al., 2009), and rhesus macaques (Higham et al., 2013) may be redundant. Blue in mandrills appears to amplify the potential information content of red (Renoult et al., 2011). However, we should not expect to find that the same evolutionary mechanisms or functions underlie different colour signals in primates. Red and blue skin colour are produced by different mechanisms, so we can expect them to be regulated by different endocrine pathways, and, potentially, to signal different qualities of the bearer, as in other taxa (e.g., Hill, 2006; Martín and López, 2009).

Pelage colour, which I have not considered here, also has the potential convey different information to skin colour. Very few studies have yet considered the functional

significance or physiological correlates of pelage coloration in primates (Clough, Heistermann, & Kappeler, 2009; Sumner & Mollon, 2003). Primate pelage colour may be more similar in mechanism and function to the well-studied plumage colour in birds (Hill, 2006) than is red skin colour, which is more labile, and more likely to reflect current state. Although birds, like primates, also show both haemoglobin-dependent red skin (Negro, Sarasola, Farinas, & Zorrilla, 2006) and structural blue skin (Prum & Torres, 2003), the majority of studies of bird colour focus on carotenoid or melanin-based plumage coloration (Hill, 2006). Furthermore, while most primate studies have examined colour itself, with the exception of the extent of red in mandrills and drills, badges of status in birds appear to be based more on the size of the colour patch than on colour itself (Senar, 2006).

Colour signals also co-occur with signals in different sensory modalities (i.e., multi-modal signals). For example, colour in mandrills is part of a suite of visual, olfactory and acoustic traits (Darwin, 1871; Osman Hill, 1970). While male mandrill colour and odour both signal age and rank, they also reflect different aspects of the male: red signals testosterone and some MHC genotypes, while odour encodes genetic diversity and genetic similarity (Setchell et al., 2011, 2009; Setchell, Vaglio, et al., 2010). Similarly, red colour and barks in male rhesus macaques have the potential to convey different information to the perceiver (Higham et al., 2013).

Finally, different signals may also be intended for different audiences, for example competitors of the same sex may be more interested in the current state of a rival, while potential mates may be more interested in underlying genetic quality, if mating decisions are based on indirect benefits that accrue to offspring, rather than direct benefits. This highlights an important aspect of the studies reviewed here. Most, but not all studies, of primate visual signals focus on the proximate mechanisms and correlates of signal production. This provides an important first step in the study of signal evolution. However, communication requires that the perceiver attends to the signal and modifies its behaviour as a result (Ruxton & Schaefer, 2011). Experimental manipulations are needed to disentangle the roles of colour signals, social familiarity and behaviour. We should also bear in mind that the signal perceived, and the perceiver's response are influenced by the perceiver's experience, environment and physiological state (Montgomerie, 2006b).

In conclusion, existing studies of the relationship between colour and competition in primates reveal interesting similarities, as well as curious differences, between the sexes and across species. Many questions remain open, but the future is bright.

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